THE ECOLOGICAL, GEOGRAPHIC, AND TAXONOMIC RELATIONSHIPS OF THE FLORA OF AN ISOLATED COLOMBIAN CLOUD FOREST, WITH SOME IMPLICATIONS FOR ISLAND BIOGEOGRAPHY

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In a companion paper (Sugden, 1982) I have described the Cloud Forest on the Serranía de Macuira (865 m), Guajira, Colombia. This forest, because of its isolation in the midst of arid lowlands, poses some interesting biogeographic problems. The Cloud Forest extends from an abrupt ecotone with dry vegetation at 550 m to the summits of the hills, forming an "archipelago" consisting of three main "islands," each approximately 5 km^2 in area, and a few outliers of less than 1 ha. The vascular flora of the Cloud Forest consists of 126 species, and the three main areas are floristically similar. Only six of these species occur frequently on the surrounding dry slopes, and none has been recorded from the lowlands of Guajira (Sugden & Forero, in prep.). The nearest moist regions (the Sierra Nevada de Santa Marta and the Sierra de Perijá) lie 250 km to the southwest. The great majority of the Cloud Forest species, including all the dominants, could have arrived in the Serranía de Macuira by long-distance dispersal (Sugden, in press a).

The purpose of this paper is to determine the origin and relationships of the Macuira Cloud Forest flora and the effects of isolation on its composition, by considering the geographic distribution, ecology, and taxonomic relationships of each species in the flora. A survey of the distributions of the species in the flora determines the geographic affinities and possible sources of recruitment; it also reveals the level of endemism in the flora, which may sometimes be a measure of the individuality of the habitat or of the extent of geographic isolation. A survey of the autecology of each species throughout its range reveals the extent to which the flora is specialized or unspecialized. Clearly, the results of each survey are of less value on their own than in relation to others; to complement and evaluate the distributional and ecological findings, it is also desirable to understand the taxonomic relationships of the species concerned and the extent to which they vary infraspecifically (White, 1971).

Because of the broad scope of this paper, a few explanatory notes on the course of the text may be useful. The methods used are briefly discussed first, followed by the general results of the surveys of distribution, ecology, and taxonomy of the Cloud Forest flora; taxonomic details for most of the species are given in the appendix. The first section of the Discussion deals

with the extent to which the flora is unique, with regard to species composition, by comparing it with published floristic data from other forests with similar climate and physiognomy. A hypothesis is then advanced for the origin of the Cloud Forest, taking into account its probable age and geographic affinities and the ecological preferences and taxonomic characteristics of its species. Finally, this hypothesis is discussed and developed in relation to some of the recent ideas and theories concerning island biology and vegetation succession, and some suggestions are made for future work.

Authors for all the species mentioned in the text are given in the companion descriptive paper (Sugden, 1982).

METHODS

Specimens of all the species of the Macuira Cloud Forest flora were examined at the herbaria of Kew (K), Oxford (FHO), the New York Botanical Garden (NY), the Missouri Botanical Garden (MO), the Smithsonian Institution (US), and the Instituto de Ciencias Naturales, Bogota (COL). In the absence of reliable published information on the majority of species, this is the only method available for determining geographic and ecological ranges. It is, however, not always satisfactory, since the labels accompanying specimens tend not to provide adequate information concerning locality or habitat. Often the degree square in which a specimen was collected cannot be determined with confidence; likewise, habitat data are of very variable quality, and altitude is frequently unrecorded. Details of habitat, if present at all, are frequently meaningless or uninformative. It was finally possible to locate about 70 percent of the specimens examined to the nearest degree square, and reliable habitat data were present on about 20 percent. Clearly, contemporary collectors must improve this situation. Altogether, some 4000 specimens were examined.

A further problem affecting the production of reliable distribution maps is that some regions are much better collected than others. Records are particularly concentrated around capital cities such as Bogota and Caracas, and in places such as Puerto Rico and the Canal Zone in Panama, where North American influence has been strong. The individual species distribution maps are not published here, but copies may be obtained from the author.

RESULTS

GEOGRAPHIC ELEMENTS

The elements of the Macuira Cloud Forest flora have been considered primarily in relation to the geographic position of the Serranía de Macuira, rather than to general patterns of distribution in the neotropical flora, not least because the latter have yet to be fully established. Thus, in the case of a species with a disjunct distribution in northern Venezuela, the Lesser Antilles, and southeastern Brazil (e.g., *Actinostemon concolor*), the Brazilian population is considered irrelevant for present purposes.

To assign species to geographic elements is not always simple, especially when the distributional records are patchy. Some species (see below) have dubious taxonomic status, and their true distribution is therefore uncertain. Also, there are inevitably some borderline cases that could be placed with justification in either of two elements. Distributions are not always as tidy as the plant geographer might wish, and there are some cases that defy categorization. The aim is simply to define some basic patterns or themes, within which there may be considerable variation.

The Macuira Cloud Forest flora has been divided into six basic elements that include all but six of the identified species. These remaining species (*Euphorbia cotinifolia, Iresine argentata, Ruellia malacosperma, Solanum dulcameroides, S. hirtum,* and *Zephyranthes tubispatha*) have not been included due to very inadequate data or uncertain taxonomy, or because their distribution has been obscured by cultivation. Of the six basic elements, five have been delimited according to large-scale differences in geographic distribution. These elements all contain species with wide distributions, while the sixth element contains species with narrow distributions. The elements are as follows:

1) Ten species, distributed throughout the neotropics and also occurring in other regions. This element can be divided into four sections according to the extra-neotropical distributions of the species: a) pantropical—*Coix lacryma-jobi,*[1] *Lycopodium cernuum, Microgramma lycopodioides;* b) tropical Africa—*Acroceras zizanioides, Gynerium sagittatum, Olyra latifolia;* 3) Malesia—*Clidemia hirta;*[1] and d) temperate America—*Erechtites hieracifolia, Erigeron bonariensis,* and *Baccharis trinervis.*

2) Forty-one species, widespread in the neotropics. This element can be divided into two sections: a) species widespread in the Caribbean area and tropical South America—*Adiantum latifolium, A. petiolatum, Chamissoa altissima, Desmodium axillare, Encyclia fragrans, Ichnanthus pallens, Jacquiniella globosa, Margaritaria nobilis, Myrcia fallax, M. splendens, Nephrolepis rivularis, Polystachya foliosa, Randia formosa, Scleria secans, Talinum paniculatum,* and *Tillandsia bulbosa;* and b) neotropical species, with continental South American range mainly restricted to the Andean and/or Guayanan regions—*Anthurium scandens, Asplenium cristatum, A. myriophyllum, Blechnum occidentale, Campylocentrum micranthum, Cestrum alternifolium, Chiococca alba, Costus guanaiensis, Equisetum giganteum, Guzmania lingulata, Guzmania monostachya, Heliconia bihai, H. latispatha, Hymenophyllum hirsutum, Malvaviscus arboreus, Peperomia glabella, Pilea microphylla, Pleurothallis ruscifolia, Polypodium phyllitidis, Rapanea guianensis, Renealmia occidentalis, Spermacoce suffrutescens, Tectaria incisa, Utricularia incisa,* and *Xiphidium caeruleum.* Three of the

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[1]Distributions due to introductions by man.

species in this element (*Randia formosa, Heliconia bihai,* and *Utricularia alpina*) are absent from Central America.

3) Seven species, mainly restricted to Central America and continental tropical South America: *Acalypha diversifolia, Alternanthera pubiflora, Liabum asclepiadeum, Persea caerulea, Psychotria alba, Stromanthe lutea,* and *Tillandsia anceps.*

4) Twelve species, mainly restricted to continental tropical South America: *Aphelandra pulcherrima, Blechnum arborescens, Costus villosissimus, Epidendrum stenopetalum, Genipa spruceana, Grammitis blepharolepis, Guzmania sanguinea, Maranta divaricata, Miconia acinodendron, Psychotria barbiflora, Rhynchospora comata,* and *Vriesea heterandra.*

5) Twelve species, mainly restricted to the Caribbean region: *Clusia rosea, Conostegia icosandra, Cyathea arborea, Dendropanax arboreus, Ficus perforata, Guapira fragrans, Miconia laevigata, Microgramma piloselloides, Myrcianthes fragrans, Ouratea nitida, Polybotrya cervina,* and *Psychotria nervosa.*

6) Twenty-three species with narrow distributions in Caribbean Venezuela and/or Colombia. This element can be divided into five geographic subcategories, the limits of which are shown in MAP 1. The largest subcategory consists of 11 species with the Serranía de Macuira as the westernmost limit of their range: *Actinostemon concolor, Croton margaritensis, Epidendrum agathosmicum, Elleanthus arpophyllostachys, Guzmania cylindrica, Hillia costanensis, Mandevilla bella, Maxillaria sophronitis, Mouriri rhizophoraefolia, Vriesea splendens,* and *Zamia muricata.* To date, none of these species has been recorded from other parts of Colombia. The distributions of these species east of the Serranía de Macuira vary in extent, the widest being that of *Vriesea splendens,* which occurs as far east as Guyana and Trinidad. They also show varying degrees of continuity and disjunction; *Croton margaritensis* has the most disjunct distribution, with one population on the Serranía de Macuira and another on Cerro San Juan,[2] Isla Margarita, 1000 km to the east.

The second subcategory in element 6 consists of six species (*Anthurium crassinervium, Coccoloba coronata, Guettarda divaricata, Machaerium humboldtianum, Philodendron erubescens,* and *Ruellia macrophylla*) distributed to either side of the Serranía de Macuira in northern Colombia and Venezuela. Of these, *Coccoloba coronata* has the widest distribution, with limits in eastern Panama and the southern Lesser Antilles. *Ruellia macrophylla* also has small disjunct populations in Cuba, Jamaica, and Peru and is included in this element only because

[2]Presently called Cerro Copey.
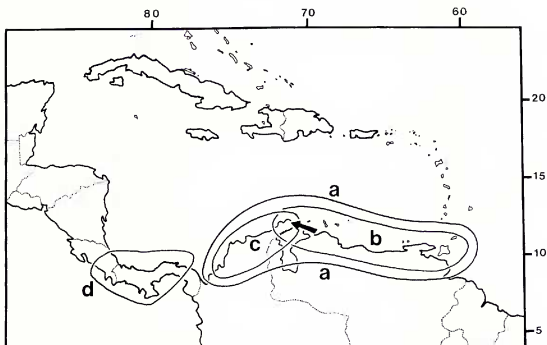
Map 1. Approximate limits of subcategories of geographic element 6. a: *Anthurium crassinervium, Coccoloba coronata, Guettarda divaricata, Machaerium humboldtianum, Philodendron erubescens, Ruellia macrophylla.* b: *Actinostemon concolor, Croton margaritensis, Epidendrum agathosmicum, Elleanthus arpophyllostachys, Guzmania cylindrica, Hillia costanensis, Mandevilla bella, Maxillaria sophronitis, Mouriri rhizophoraefolia, Vriesea splendens, Zamia muricata.* c: *Cynanchum atrovirens, Rudgea marginata, Scutellaria verecunda.* d: *Stemmadenia minima, Schlegelia fuscata.* Arrow, Serranía de Macuira.

the Colombian and Venezuelan parts of its range are clearly the most substantial.

The third subcategory consists of three species (*Cynanchum atrovirens, Rudgea marginata,* and *Scutellaria verecunda*) that are restricted to northern Colombia, with the Serranía de Macuira as their northernmost limit.

The fourth subcategory consists of two species (*Stemmadenia minima* and *Schlegelia fuscata*) that have not previously been recorded outside eastern Central America; before this disjunction can be proved genuine, however, further collections are required from the intervening Sierra Nevada de Santa Marta. Also, there are some taxonomic problems associated with these species (see APPENDIX, and below).

The fifth subcategory contains a single species, *Cordia macuirensis*, which is the only species in the flora to have possible endemic status. It is closely related and similar in appearance to *C. curassavica*, which is widespread in the surrounding dry lowlands and may simply be an incipient species (see APPENDIX).

The sixth element is not delimited in the same strict sense as the first five, since it represents a variety of distribution patterns. The species in this element have only the relatively restricted nature of their distri-
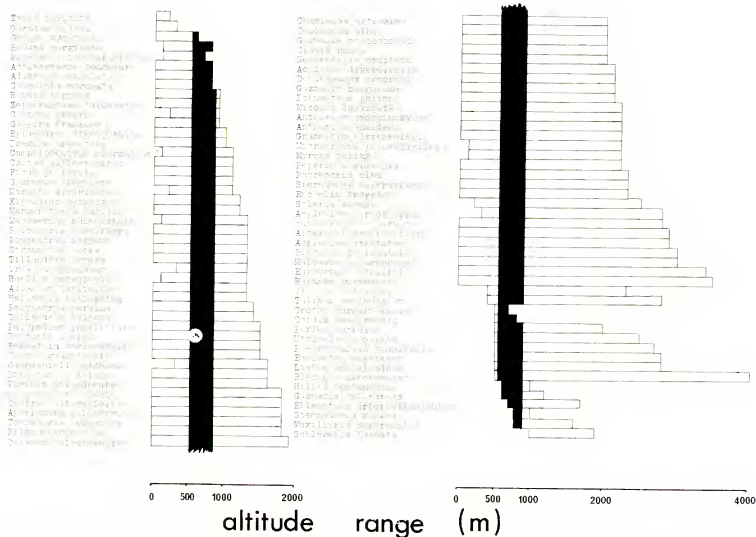
FIGURE 1. Altitudinal ranges of Macuira Cloud Forest species. Black bar represents altitudinal limits of Macuira Cloud Forest.

butions in common and have been grouped together for interpretative purposes only. Strictly, the subcategories of element 6 are elements in themselves.

Ecological Distribution

It is not practical to divide the flora into precise ecological elements, partly because of the wide habitat preferences of many of the species, and partly due to the variation in quality of the sources of information. The extent to which the flora is specialized to low-altitude cloud forest can be partly determined by examining the range of altitude and types of vegetation across which the species are distributed. The geographic evidence has already indicated that the level of specialization must be quite low.

In Figure 1 the altitudinal ranges are shown for the ninety-one species for which there are sufficient data. Most of the species occur in lowland habitats, and only sixteen are restricted to montane regions. Of these sixteen species, eight (*Cordia macuirensis, Croton margaritensis, Elleanthus arpophyllostachys, Guzmania cylindrica, Hillia costanensis, Maxillaria sophronitis, Schlegelia fuscata,* and *Stemmadenia minima*) are confined to low-altitude cloud forests, and all have relatively restricted geographic distribution.

Of the large proportion of species occurring in lowland habitats, only nine do not occur at elevations higher than that of the highest peak of the Serranía de Macuira (865 m); the remainder occur at elevations both higher and lower than the limits of the Macuira Cloud Forest. Sixty-six species occur over altitudinal ranges of 1000 m or more; thirty-three of these occur over ranges of 2000 m or more, with *Rapanea guianensis* having the widest range (0–3500 m).

The range of habitats in which each species has been recorded is given in Table 1. The 11 habitat types included are grouped under the broad headings of Lowland, Montane, and Disturbed. The lowland habitats include littoral zones, savanna and cerrado, dry forest, moist forest (including lowland rain forest), and swamp. The montane habitats include moist (and cloud) forest and páramo. Disturbed habitats include secondary vegetation, banks of rivers and streams, exposed rocky hillsides, and ravines, without regard to altitude. In the present context, the definition of these terms must be somewhat loose because of the imprecise nature of basic information. A lowland species is here defined as one that occurs from at or near sea level to no more than 1000 m, while a montane species is one occurring only above 500 m; the overlap is necessary due to the "Massenerhebung" effect, or the lowering of montane vegetation belts on isolated mountains and ridges (Grubb, 1971). Disturbed habitats are difficult to define precisely; disturbance can be broadly regarded as the combination of mechanisms that limit plant biomass by causing its partial or total periodic destruction (Grime, 1979). Disturbance may be regular, as in the case of riverbanks subject to flooding or landslides, or may have occurred but once, as in a tract of land cleared for human use and subsequently abandoned.

In Table 1 the species are listed according to life form, and their occurrence in any given habitat is recorded on the basis of presence or absence.

TABLE 1. **Ecological distribution of Macuira Cloud Forest species.***

	LOWLAND HABITATS					MONTANE HABITATS		DISTURBED HABITATS			
	Littoral	Savanna/Cerrado	Dry Forest	Moist Forest	Swamp	Cloud Forest/Moist Forest	Paramo	Secondary	River banks	Exposed rocky hillsides	Ravines
CANOPY TREES[†]											
Blechnum arborescens						+	+		+	+	
Cyathea arborea						+					+
Stemmadenia minima						+					
Dendropanax arboreus			+	+							
Euphorbia cotinifolia		+						+			
Margaritaria nobilis			+	+				+	+		
Persea caerulea						+					+
Conostegia icosandra		+	+	+				+			
Miconia acinodendron				+		+		+	+		
Miconia laevigata						+		+	+	+	+
Mouriri rhizophoraefolia			+								
Ficus perforata	+	+	+	+				+	+		
Rapanea guianensis	+	+	+		+	+		+			
Myrcia fallax		+		+				+			
Guapira fragrans	+		+			+					

Ouratea nitida				+						
Coccoloba coronata		+					+	+		
Genipa spruceana			+	+				+		
Randia formosa	+	+	+	+			+			

UNDERSTORY SHRUBS AND COARSE HERBS

Equisetum giganteum				+			+	+		
Maranta divaricata			+		+					
Stromanthe lutea					+			+		
Heliconia bihai			+					+		
Heliconia latispatha			+	+			+	+		
Costus guanaiensis			+	+	+		+			
Costus villosissimus			+					+		
Renealmia occidentalis					+			+		
Alternanthera pubiflora	+		+				+	+		
Chamissoa altissima			+	+	+		+	+		
Acalypha diversifolia	+		+		+		+			
Actinostemon concolor			+		+					+
Croton margaritensis					+					
Malvaviscus arboreus	+		+	+	+		+			
Clidemia hirta							+	+		
Chiococca alba	+	+	+				+	+		
Psychotria alba			+	+	+					
Psychotria barbiflora			+				+			
Psychotria nervosa	+				+					
Spermacoce suffrutescens		+			+		+	+	+	
Cestrum alternifolium	+	+	+		+		+	+		

GROUND LAYER

Adiantum latifolium		+	+	+			+	+	+	+
Adiantum petiolatum		+	+	+				+		+

TABLE 1 (*continued*).

	LOWLAND HABITATS				MONTANE HABITATS		DISTURBED HABITATS			
	Littoral	Savanna/Cerrado	Dry Forest	Moist Forest	Swamp	Cloud Forest/Moist Forest	Paramo	Secondary	River banks	Exposed rocky hillsides	Ravines
Asplenium cristatum					+	+		+		+	
Asplenium myriophyllum						+			+		
Blechnum occidentale			+	+		+		+	+	+	
Polybotrya cervina				+		+					+
Tectaria incisa								+	+		+
Rhynchospora comata			+	+		+			+		
Scleria secans			+		+	+		+			
Ichnanthus pallens		+		+	+	+		+	+		
Xiphidium caeruleum			+	+				+	+		
Campylocentrum micranthum			+	+				+		+	
Encyclia fragrans		+	+	+		+					
Ruellia malacosperma									+		
Liabum asclepiadeum									+		
Pilea microphylla					+			+	+	+	

EPIPHYTES

Grammitis blepharolepis				+							

Species									
Hymenophyllum hirsutum						+			+
Nephrolepis rivularis				+	+	+			
Microgramma piloselloides						+			
Polypodium phyllitidis				+					+
Anthurium scandens				+		+	+		+
Guzmania cylindrica						+			
Guzmania lingulata				+	+	+		+	
Guzmania monostachya	+		+	+		+			
Guzmania sanguinea				+		+			
Tillandsia anceps				+	+	+			
Tillandsia bulbosa		+	+			+			
Vriesea heterandra						+			
Vriesea splendens				+	+	+		+	
Campylocentrum micranthum			+	+			+	+	
Elleanthus arpophyllostachys						+			
Jacquiniella globosa				+			+	+	
Maxillaria sophronitis						+			
Pleurothallis ruscifolia				+		+			
Polystachya foliosa		+	+	+		+			+
Utricularia alpina					+	+	+	+	
Peperomia glabella	+		+	+	+	+			
Hillia costanensis						+			

GROUND-ROOTED CLIMBERS AND SCRAMBLERS

Species									
Iresine argentata				+		+			
Mandevilla bella									+
Cynanchum atrovirens		+							
Schlegelia fuscata						+			

*Derived mainly from information accompanying herbarium specimens.

†Species listed in same order and under same categories as in *table 3* in Sugden (1982). Category under which each species is listed refers to its life form in Macuira Cloud Forest *only* (e.g., *Blechnum arborescens* is not a canopy tree, by definition, in páramo).

Species missing from the list include those for which information was not available, as well as the widespread weedy species in geographic element 1; the latter tend to occur in early secondary vegetation. The table thus includes 82 species, or 66 percent of the flora. The ecological distribution of each life form, taken from information in TABLE 1, is depicted in FIGURE 2.

The remarkable general feature of these results is the wide ecological distribution of most of the Macuira Cloud Forest species; there are only eighteen that do not occur in more than one of the three major habitat groups. These include the eight species restricted to low-altitude cloud forest. Of the remaining ten, *Clidemia hirta*, *Ruellia malacosperma*, *Liabum asclepiadeum*, and *Mandevilla bella* are apparently restricted to disturbed habitats, *Dendropanax arboreus* to lowland dry and moist forest, *Ouratea nitida* to lowland swamps, *Grammitis blepharolepis* to lowland moist forest, *Cynanchum atrovirens* to dry scrub and lowland savanna, and *Micrograma piloselloides* and *Vriesea heterandra* to moist montane forest. However, *Micrograma piloselloides* occurs as low as 100 m, as shown in FIGURE 1, so these data should be viewed with some caution.

That so many species should occur across such a wide range of habitat shows that the flora is largely composed of "generalist" rather than "specialist" species. Moreover, the fact that 56 of the 82 species listed in TABLE 1 occur in disturbed habitats suggests that the flora has a strong colonizing or pioneering element. The histograms in FIGURE 2 demonstrate the high proportion of species from disturbed habitats in each life form (with the exception of the epiphytes, where the proportion from undisturbed habitats is higher).

TAXONOMY

Alongside the trends of wide geographic distribution and ecological amplitude, there appears to be a tendency in the flora toward species with substantial infraspecific variation. There are at least 34 variable species in the flora (see APPENDIX), most of which are widely distributed. There are examples of variation at the subspecific (*Encyclia fragrans*, *Psychotria nervosa*) and the varietal levels (*Guzmania lingulata*, *Vriesea splendens*), and of continuous variation (*Anthurium scandens*, *Dendropanax arboreus*, *Ficus perforata*), although these different kinds of variation must in part reflect the individual preferences of taxonomists. The evidence is not sufficient to determine whether ecotypic variation occurs, but such patterns might emerge given more detailed field studies and more extensive collections; certainly, some of the variation has a geographic basis (see APPENDIX). Nevertheless, there are at least 15 species, some with wide distribution, that exhibit little or no infraspecific variation; these include *Aphelandra pulcherrima*, *Costus villosissimus*, *Epidendrum stenopetalum*, *Equisetum giganteum*, *Guzmania monostachya*, *Heliconia latispatha*, *Hillia costanensis*, *Mouriri rhizophoraefolia*, *Ouratea nitida*, *Peperomia glabella*, *Ruellia macrophylla*, *Talinum paniculatum*, *Tillandsia anceps*, *T. bulbosa*, and *Vriesea heterandra*.

Among the species with narrower ecological and geographic distribution, there are several with dubious taxonomic status (see APPENDIX); these may
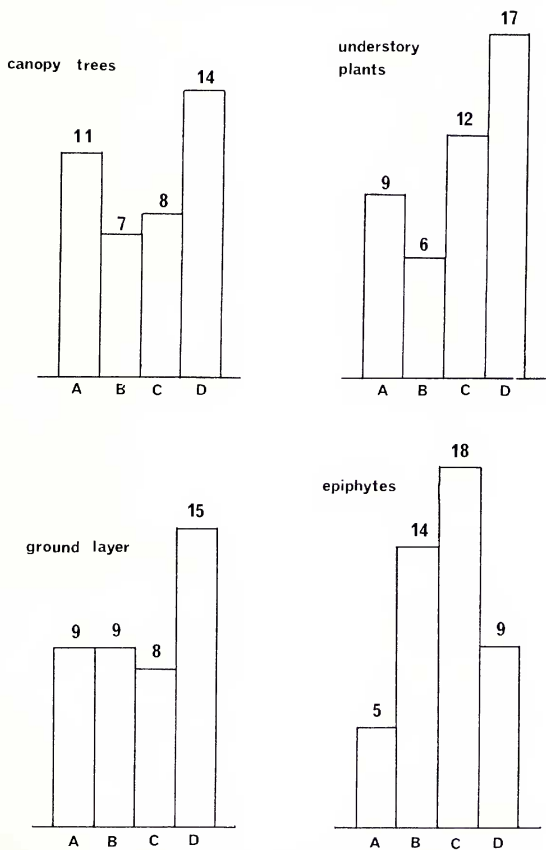
FIGURE 2. Histograms of ecological distribution of Macuira Cloud Forest species, drawn from data in Table 1. Letters indicate habitat: A, dry; B, moist lowland; C, moist montane; D, disturbed.

be no more than infraspecific forms of more widely distributed taxa. There are others, also with narrow distribution, that are members of geographically replacing species complexes or superspecies *sensu* Mayr (1963) and F. White (1979), and these may have evolved recently from common ancestral stock (see APPENDIX).

The taxonomic status of the 38 species not discussed in this section or in the APPENDIX has not been examined, either because there was no information available, or because (in the case of species with wide extra-neotropical distribution) information was not sought. This does not, however, affect the general conclusion that the flora has a large component of variable species—a component that may become larger when more data become available. An expansion of this component would also reduce the proportion of narrowly distributed species, thus reinforcing the evidence that the Macuira Cloud Forest flora is composed largely of opportunist species with wide ecological and geographic distribution.

DISCUSSION

COMPARISON WITH OTHER CLOUD FORESTS

Before consideration of the origin of the Macuira Cloud Forest, it is necessary to consider briefly the extent to which its flora is unique, both in species composition and in the characteristics (low species diversity, lack of specialization, low endemism, and high dispersibility) described above and in Sugden (in press). Comparative discussion will be restricted mainly to those neotropical forests that most closely resemble the Macuira Cloud Forest in terms of physiognomy, area, climate, and isolation by arid lowlands. The two forests that appear to fulfill these criteria (see Sugden, 1982) are in coastal Venezuela, one on the summit of Cerro Santa Ana, Península de Paraguaná, Edo. Falcón, and one on Cerro San Juan, Isla Margarita, Edo. Nueva Esparta. Floristic accounts for these two mountains have been produced respectively by Tamayo (1941) and Johnston (1909), although Tamayo's list is incomplete due to the short duration of his visit to Cerro Santa Ana.

Specific and generic diversity are similar on the Serranía de Macuira and Cerro San Juan. The somewhat higher number of species on the latter (166, vs. 126 on the Serranía de Macuira) is almost entirely the result of a larger complement of pteridophytes (55 species, vs. 19 on the Serranía de Macuira)—an interesting feature for which there is no ready explanation. The numbers of species of other vascular plants are almost equal (111 on Cerro San Juan, 106 on the Serranía de Macuira), and the relative proportions of monocotyledons and dicotyledons are also similar in the two localities. As on the Serranía de Macuira, the ratio of species to genera is low on Cerro San Juan; this also applies to Cerro Santa Ana. Those genera that are represented by two or more species are generally ferns and monocotyledons; among the dicotyledons only *Miconia* and *Psychotria* have more than one species on each mountain.

There is relatively little overlap in species composition between the three cloud forests. Of the 56 species of vascular plants recorded by Tamayo (1941) on Cerro Santa Ana, and the 155 species in Johnston's (1909) list for Cerro San Juan, only 18 percent and 11 percent, respectively, are shared with the Macuira Cloud Forest. Only three species (*Guzmania lingulata, Vriesea splendens,* and *Utricularia alpina*) are known from all three mountains. Thus, there is no distinct association of species that can be considered characteristic of these cloud forests. At the generic level there is more overlap, with Cerro Santa Ana and Cerro San Juan each sharing ca. 50 percent of their genera with the Macuira Cloud Forest. Genera that occur on all three mountains are *Elaphoglossum, Microgramma, Polypodium, Blechnum, Hymenophyllum, Lycopodium, Scleria, Guzmania, Tillandsia, Epidendrum, Piper, Clusia, Myrcia, Miconia, Utricularia, Hillia,* and *Passiflora;* with the exception of *Hillia,* all are large genera with wide neotropical distributions. It would probably be wrong to conclude that there is a distinct core of genera characteristic of these cloud forests since most of them can be found in most moist neotropical forests.

There are few instances of closely related species replacing one another on the three mountains. Between the Serranía de Macuira and Cerro San Juan, vicariousness of this kind is confined mainly to herbaceous and epiphytic genera (e.g., *Lycopodium, Rhynchospora, Scleria, Anthurium, Tillandsia, Heliconia, Maranta, Stromanthe,* and *Epidendrum*) rather than the dominant woody genera. The presence on Cerro San Juan of families not represented in the Macuira Cloud Forest (Palmae, Commelinaceae, Liliaceae, Dioscoreaceae, Iridaceae, Proteaceae, Aristolochiaceae, Oxalidaceae, Rutaceae, Marcgraviaceae, Violaceae, Flacourtiaceae, Begoniaceae, Thymelaeaceae, Combretaceae, Ericaceae, Gentianaceae, Gesneriaceae, and Campanulaceae) supports the conclusion that the similarity of these cloud forests has a weak floristic basis.

In spite of these compositional differences, the three floras have several important characteristics in common, as well as their similar species diversity and physiognomy. Endemism is low in all three cases. No endemic species appear to have been recorded from Cerro Santa Ana. Although Johnston's (1909) original list for Cerro San Juan contained eight endemics (5 percent of the flora), four belong to large genera with many variable species (*Passiflora, Piper,* and *Pleurothallis*), one has been reduced to a subspecies of a widespread variable species (*Chiococca alba;* see APPENDIX), and one (*Croton margaritensis*) has since been found on the Serranía de Macuira. Johnston confidently expected that many of the 42 new species described from his entire collection from Isla Margarita would be found in other regions then not yet visited by collectors.

The levels of endemism in various other less isolated and more extensive neotropical cloud forests are apparently higher than those in the Serranía de Macuira or Cerro San Juan. Steyermark (1975) found that 6 percent of the flora of the cloud forest on the Sierra de San Luis, Edo. Falcón, Venezuela, was endemic to the mountain, while an additional 29 percent had been recorded previously only from the Cordillera de la Costa to the east. Although

the San Luis cloud forests are isolated by arid lowlands, they are more extensive and have a greater diversity of habitats than the Macuira Cloud Forest. Lewis (1971) estimated that about 25 percent of the vascular plant species in Panamanian and Colombian cloud forests are endemic to either particular localities or vegetation types, indicating a greater degree of specialization to the habitat than is shown by the Macuira or San Juan floras. This high figure may, however, be due in part to weak taxonomy in many groups and to the tendency to expect that isolated, unexplored mountains are bound to support new species. Hodge (1954) showed that the elfin forests in Dominica support more endemics and species of restricted distribution than do other vegetation formations on the island. On the other hand, Howard (1973) observed that elfin forests in the Antilles support few endemics, most species being widespread in comparable habitats—in spite of the high proportion (32 percent) of species from the Elfin Forest on Pico del Oeste, Luquillo Mountains (Howard, 1968) that are endemic to Puerto Rico. Clearly, it is unwise to generalize in these matters since there is so much variation between localities and because the term "endemism" is often loosely applied in the literature.

Cursory inspection of the floristic lists from Cerro Santa Ana and Cerro San Juan indicates that the dispersibility of the cloud forest species is generally good, as in the Serranía de Macuira (Sugden, in press b). In both localities there is a high proportion (40–50 percent) of wind-dispersed epiphytes and herbs; the majority of the trees and shrubs have fruits and seeds that suggest endozoic dispersal by birds.

Thus, while the Macuira Cloud Forest is physiognomically similar to some other low-altitude isolated cloud forests, and although its flora bears some gross resemblances to the floras of these forests, it consists of a unique assemblage of species that do not form a distinct association or community in any other situation. This is as true of the dominant or common species as it is of the entire flora.

A final cautionary note should be added to the effect that the above comparisons (especially those concerning the floristics of Cerro Santa Ana) have relied partly on incomplete data. It will probably be necessary to refine and update these comparisons in the light of the new information being gathered in the current Venezuelan floristic projects in Edo. Falcón and Isla Margarita.

Origin of the Macuira Cloud Forest: A Hypothesis

HISTORICAL ORIGIN. The lack of endemic species in the Cloud Forest clearly demonstrates that the flora is not even a partial relict comprising species representing ancient groups that have become extinct or drastically reduced in their distribution elsewhere. The only possible exception to this is the cycad *Zamia muricata*, but the taxonomic relationships of this species have not received adequate treatment and its evolutionary status is unknown. The lack of endemics also demonstrates that isolation has not been effective, either spatially or temporally, in allowing the evolution of species unique to the Serranía de Macuira (with the possible exception of *Cordia macuirensis*).

The Cloud Forest also does not appear to be an ecological refuge in the sense of the Pleistocene Amazonian refugia originally proposed by Haffer (1969), in which widespread species characteristic of lowland moist forest were constricted into isolated pockets during drier climatic periods. The lack of endemics, together with the wide ecological amplitude and high dispersibility of most of the Cloud Forest species, argues against the notion that they were once widespread in the Guajira lowlands and have been forced to the summits of the Serranía de Macuira by increasing aridity.

An additional important negative point is that the prominent colonizing component of the flora is not the result of recent disturbance of the Cloud Forest. Human interference on the upper slopes of the Serranía de Macuira is, and always has been, very limited. There are several features of the Cloud Forest that tend to confirm this view. The most striking are the floristic and physiognomic uniformity both within and between the three principal "islands" of Cloud Forest on the Serranía, and the very small number of species that could owe their presence to dispersal by man or livestock (Sugden, in press b).

Since the Cloud Forest is not an evolutionary relict or an ecological refuge, an alternative hypothesis concerning its origin is necessary. The prevalence of widespread species characteristic of disturbed habitats suggests that at some time the conditions on the summits of the Serranía changed in some manner favorable for colonization by successional species of this kind. This change would of necessity have been from a dry to a wet climate rather than from a very wet to a less wet climate; the latter would have resulted in an ecological refuge, which has already been shown to be unlikely. It would also have been a change from a seasonal climate, such as prevails over the Guajira lowlands at present, to a less seasonal climate with a more even distribution of annual precipitation. This could have occurred as a result of an increase in the frequency, regularity, and duration of periods of cloud cover and a lowering of the average cloud base level.

A situation may therefore be envisaged in which the dry forest types presently occurring immediately below the Cloud Forest (Sugden, 1982) extended to the highest summits of the Serranía de Macuira, as they do now in the neighboring Serranía de Jarara. As the frequency and duration of cloud cover increased, reaching the critical point at which Cloud Forest can be maintained, propagules of Cloud Forest species carried by air currents and by birds were able to germinate successfully and to establish populations on the summits of the hills. These populations gradually expanded as the critical level of cloud cover extended down the hills to its present altitude. At the same time, the dry forest species—unable due to their seasonal growth patterns to compete in the wetter and darker conditions prevailing in the advancing Cloud Forest—were forced down the slopes.

As the Cloud Forest spread down the slopes from the summits of the Serranía, its area increased and its topographical habitats diversified (see Sugden, 1982, for a summary of present habitat diversity in the Cloud Forest), permitting the establishment of more species—particularly the epiphytes and coarse herbs that are the likely beneficiaries of an increase in habitat diversity

(Sugden, in press a). The development of streams and small swamps in the gullies provided a habitat suitable for large monocotyledons such as *Heliconia, Costus, Renealmia, Maranta,* and *Dieffenbachia.* The more prolonged and heavy cloud cover toward the summits (Sugden, 1982, *table 1*) permitted the establishment of populations of epiphytic species with a high moisture requirement (e.g., *Vriesea splendens* (Sugden, in press a)). Other epiphytes, such as *Tillandsia anceps* and *Guzmania monostachya,* which are tolerant of the drier conditions prevailing toward the lower limit of the Cloud Forest (Sugden, in press a), maintained their densest populations nearer to the retreating edge of the dry forest. Because moisture supply is not such a critical factor in the distribution of trees and shrubs (Grubb & Tanner, 1976), the dominant woody species maintained their presence throughout the Cloud Forest as it expanded.

If events of this kind occurred, then the remaining questions concern when the sequence was initiated and from where the flora was derived. While there is no firm evidence that the Macuira Cloud Forest has not been present for a very long time (i.e., since before the Pleistocene), this is unlikely for several reasons. The flora itself has no features that indicate great age. Furthermore, there is evidence for some recent climatic changes that would have affected the regime of cloud cover on the Serranía de Macuira. Although there are no data concerning the climatic history of Guajira itself, there have been events (e.g., the drier, more seasonal period ca. 8000–4000 years B.P., and the rise in sea level that has continued since the end of the last glacial epoch 12,500 years B.P. (see Sugden, in press b, for details and references)) in neighboring regions that could have accompanied a reduction in cloud cover to a level below that required to sustain the Cloud Forest. Such a reduction could have resulted in a more seasonal climate, a higher cloud base level, less prolonged daily periods of cloud cover, or a combination of any of these. In short, the existence of the Cloud Forest is precarious, and it is unlikely that the requisite climatic conditions have been constant for many millenia, let alone geologic eras. It is not unreasonable to conclude that the sequence of events proposed above began only a few thousand years ago.

This hypothesis does not preclude the existence of a moist summit forest at earlier times. Such a forest, as a vegetation type rather than a floristic assemblage, may have undergone a cycle of colonization and extinction in the Serranía de Macuira in response to climatic fluctuations during the Quaternary and before, although the present flora provides no such evidence. It also does not preclude the possibility that colonization and local extinction are occurring at present. There are a number of species, including *Blechnum arborescens, Cyathea arborea, Equisetum giganteum, Grammitis blepharolepis, Microgramma piloselloides, Dichaea* sp., *Elleanthus arpophyllostachys, Encyclia fragrans, Jacquiniella globosa, Erigeron bonariensis,* and *Psychotria barbiflora,* that were encountered only once or twice, either as single individuals or in clumps, and there may be more rare species that were never encountered during this study. Such rarity suggests that these species are scarcely established in the Cloud Forest, although it is impossible to say whether they are remnants of a larger population on the verge of local ex-

tinction or the newly colonized forebears of a future larger population.

A similar hypothesis has been proposed for the origin of the moist upland flora of the Galapagos archipelago, which was mostly derived through long-distance dispersal from the mainland of South America (Johnson & Raven, 1973; Porter, 1976). The upper slopes of the higher islands in the Galapagos receive substantially more rainfall, and sometimes more cloud cover, than the lower slopes. The percentage of the flora that is endemic to the archipelago is lower in the moist uplands than in the arid and transition zones. On the basis of this and evidence from core samples of Galapagos lake sediments that indicate a much drier climate 30,000–10,000 years B.P., Johnson and Raven (1973) suggest that most of the species of the upland flora have arrived from the mainland during the last 10,000 years. The majority of these species are adapted for endozoic dispersal by birds (Johnson & Raven, 1973; Porter, 1976).

GEOGRAPHIC AFFINITIES. The evidence concerning the geographic derivation of the Cloud Forest flora is perhaps less equivocal. Because the flora does not closely resemble the floras of other cloud forests on the Caribbean coast of South America or the Antilles, it clearly does not fit any wider chorological pattern. Also, the various distributions of the relatively restricted species (element 6) show that the present complement of species in the flora cannot be the result of derivation from any single source. Rather, there are definite relationships with regions to the west, the southwest and south, and the east, as evinced by the species in element 6 with the Serranía de Macuira as one of their geographic limits of distribution. This indicates the existence of long-distance dispersal routes from all the neighboring parts of the South American mainland, as well as from Panama.

That some species may have been derived from the Antilles is also possible. *Cyathea arborea*, apart from one dubious record from Caracas, is known only from the Antilles (Tryon, 1979) and Isla Margarita (Steyermark & Ortega, 1981). Its propagules may have arrived in the Serranía de Macuira borne on the trade winds blowing from the Lesser Antilles. There are no other wind-dispersed species for which such a derivation would have to be invoked, but the possibility cannot be ruled out. Also, some of the migratory birds from the Antilles and beyond may make their first landfall in the region of the Serranía de Macuira (Sugden, in press b); again, however, there are no bird-dispersed species in the Cloud Forest flora that demand such an origin.

There are several indications that the greater proportion of the flora may have been derived from northern and northwestern Venezuela. The largest subcategory in geographic element 6 (species with restricted distributions) comprises species that have their westernmost outpost in the Macuira Cloud Forest; this perhaps constitutes evidence for more migration from northern Venezuela than from other mainland regions. Steyermark (1975) reached a similar conclusion regarding the derivation of the flora of the Sierra de San Luis, Edo. Falcón, Venezuela. The large element of Venezuelan endemics in the San Luis flora was mainly derived from the Cordillera de la Costa,

which was in existence before the uplift of the Sierra de San Luis. About 30 percent of the flora had not previously been recorded outside the Cordillera de la Costa. This appears to be good evidence for the existence of a migration route from east to west. A smaller proportion of the San Luis flora (ca. 12%) was apparently derived from the Andes to the south. If the Cordillera de la Costa retained its moist climate throughout the Pleistocene and was, as Prance (1974, 1977) has suggested, a refuge for moist forest species, then it is indeed likely to have been an important source of species colonizing younger moist forests to the west. The strong easterly component of the prevailing winds in Guajira and northern Venezuela is probably an important factor contributing to the affinities between the floras of the two regions. This would affect not only those plants with wind-dispersed propagules, since migratory and vagrant birds tend to travel with the wind rather than against it. Indeed, both wind- and bird-dispersed species in the Macuira Cloud Forest demonstrate the Venezuelan connection.

Further evidence for a stronger link with northern Venezuela than with other regions is provided by some of the animal groups that have been investigated in the Serranía de Macuira. Many of the butterflies of the Cloud Forest are probably of Venezuelan derivation (J. L. B. Mallet, pers. comm.). Examination of the distribution of birds recorded by Marinkelle (1970) in the Serranía reveals, out of a total of 38 narrowly restricted taxa, 19 species and subspecies restricted mainly to northern Venezuela and the Serranía de Macuira. These data must be viewed with caution, however, partly because the collections were made over short periods and are probably incomplete, and partly because the taxonomic criteria and the factors affecting the distribution of these organisms are different from those affecting plants.

The species of restricted distribution that have arrived in the Serranía de Macuira from the south and west are fewer than those that are apparently derived from Venezuela. Successful dispersal events in this direction might be expected to be restricted to the brief rainy season, when the winds blow mainly from the south.

Since the bulk of the flora is widely distributed, it cannot be used to interpret the geographic derivation of the component species. There is no reason to suppose, however, that the patterns of dispersal and migration of the widespread species are governed by factors different from those affecting species of more narrow distribution. Given the possible existence of an important migration route from northern Venezuela, mediated by the prevailing winds, it is likely that most of the widely distributed species in the Macuira Cloud Forest flora have a Venezuelan derivation.

To summarize, it has been postulated that the Cloud Forest was formed *de novo* following a recent climatic change, and that the flora has been derived from various parts of the South American mainland (especially northern Venezuela) and possibly the Antilles. This hypothesis is based on the assumptions that there is a critical amount of cloud cover below which the Cloud Forest cannot be sustained, and that long-distance dispersal can be held accountable for the presence of virtually all the species in the flora. Habitat diversity increased as the Cloud Forest expanded, with favorable

consequences for the epiphytic and herbaceous communities but with little effect on the distribution of the woody species within the Cloud Forest. It is suggested that the homogeneity of the woody flora is the result of a wider tolerance of soil moisture levels.

THE CLOUD FOREST, ISLAND BIOLOGY, AND SUCCESSION: CONCLUSIONS

The hypothesis for the origin of the Cloud Forest flora is based on inference and speculation concerning historical events, and although plausible, it is clearly untestable. Also, it does not by itself account for several of the more interesting features of the Macuira Cloud Forest, in particular, the relatively low number of species, the uniqueness of the assemblage of species, and the presence of a large pioneering contingent in an apparently mature forest. These issues may profitably be considered in light of some of the current ideas concerning insular biogeography and vegetation succession; in so doing, one can arrive at some predictions and possibilities that could be investigated by further fieldwork.

The Serranía de Macuira, in spite of its modern lowland links to other mountain ranges, is analogous to oceanic islands in several ways. Oceanic islands and archipelagoes are characterized by their permanent isolation, dating from their genesis, from continental regions. The Serranía de Macuira has never had a high-altitude connection to either the Andes or the Sierra Nevada de Santa Marta, and the geologic evidence (Macdonald, 1964; Lockwood, 1965) indicates that faulting and erosion separated it from the neighboring Serranía de Jarara during the Oligocene. Indeed, it was a true island during the Pliocene, when a major marine transgression inundated the lowlands of Guajira. Also, there is no element in the Cloud Forest flora that requires a lowland connection to explain its presence. The risks of drawing parallels between oceanic islands and the upper slopes and summits of continental mountains have been discussed by F. White (1971) and by Mabberley (1979); due to climatic fluctuations, montane vegetation belts can contract and expand, sometimes forming extensive connections with those of other mountains, and floristic isolation may be reduced or broken down altogether. The insularity of the Macuira Cloud Forest, however, appears to be permanent and genuine (Sugden, in press b).

The hypothesis for the origin of the flora entailed an initial disturbance—that is, a climatic change that permitted the establishment of the Cloud Forest—followed by a gradual retreat of the drier formations down the slopes of the Serranía. P. S. White (1979), drawing partly on the ideas of Grime (1977, 1979), has stressed that assemblages of species in disturbed habitats tend to be transient and locally unique—i.e., they are not repeated in space. Insular species assemblages sometimes show a similar lack of organization into well-defined communities (Linhart, 1980). Moreover, species of disturbed habitats tend to be tolerant of wide ecological extremes, which is exactly the case with the bulk of the Macuira Cloud Forest flora. However, if disturbance ceases and there are no species of later successional stages to

take the place of the pioneers (Mabberley, 1979), then the succession is curtailed and the pioneers form the "climax" (P. S. White, 1979). In the case of the Macuira Cloud Forest, isolation may have reduced the frequency of successful dispersal events so as to prevent the establishment both of species of later successional stages and of other pioneering species with less mobile propagules.

It may be suggested that the uniqueness of the assemblage of species in the Macuira Cloud Forest (and of the equally individual assemblages on the summits of Cerro Santa Ana and Cerro San Juan) is simply the result of colonization by a random subset of taxa with good dispersibility and wide ecological tolerance. Random colonization of this kind is regarded by some as an important determinant of island species composition (Simberloff, 1978; Connor & Simberloff, 1978, 1979). The size and composition of this subset must initially have been constrained by the ability of the propagules to germinate and eventually to establish a population of reproducing adults in the conditions prevailing in the Cloud Forest. The establishment of such a population might be expected to be favored by an ability to produce large quantities of seed (and/or vegetatively propagated individuals) and by unspecialized pollination systems that reduce competition for pollinators. Early successional species often have less-specialized pollination mechanisms than species of later successional stages (Parrish & Bazzaz, 1979); similarly, island species may have pollination mechanisms that are unspecialized relative to those of mainland species (Linhart & Feinsinger, 1980). Groups with efficient dispersal may be unable to establish populations in new areas if their pollinators are absent (Carlquist, 1967). It is interesting in this context that most of the Cloud Forest species with large, showy (specialized?) flowers (*Stemmadenia minima, Mandevilla bella, Hillia costanensis*) have restricted distributions (element 6), while most of the widely distributed species have small, apparently unspecialized flowers.

Reproductive biology would probably not be the sole determinant of the composition of the community. There is no reason to assume that propagules of a wide variety of species did not continue to arrive in the Serranía de Macuira by long-distance dispersal following the appearance of the Cloud Forest, and do not continue to do so now. If conditions remain the same, later arrivals may have less chance of establishment because of the reduction in available regeneration niches caused by earlier arrivals. The availability of regeneration niches is a significant factor affecting species richness (Grubb, 1977), and the frequency of disturbances affects the chances of establishment of pioneer species (Grime, 1979; P. S. White, 1979; Bazzaz & Pickett, 1980). The frequency of gaps in the Cloud Forest is low, possibly due to the slow growth rates imposed by nutrient stress and a concomitant low rate of disturbance. It may be significant that some of the extremely rare species in the flora were found in gaps rather than under a closed canopy. *Cyathea arborea* and *Equisetum giganteum* were each encountered once, on open, sunlit streambanks, and *Erigeron bonariensis* was found on a small, open patch of ground at the summit of Cerro Huarech (see Sugden, 1982, *map 3*) that had been cleared for a helicopter landing site some years pre

viously and had subsequently been abandoned. Large-scale disturbances (such as hurricanes or earthquakes) that could afford opportunities for colonization by new species have not been recorded in the region.

There is a persistent pool of seedlings and young plants of the dominant tree species in the Cloud Forest. In a restricted survey of 98 m^2 on a sheltered ridge at 650 m, there were 218, 100, and 73 seedlings less than 20 cm tall of *Guapira fragrans*, *Rapanea guianensis*, and *Myrcianthes fragrans*, respectively. It is not known whether these seedlings remain in a "dormant" post-germinative state awaiting a light gap caused by a fallen tree, as do many species of later successional stages in lowland rain forest (Whitmore, 1978; Grime, 1979), or whether they grow continuously. In either case, however, they would have a great numerical advantage over seedlings germinated from newly arrived propagules. Low species diversity in the Macuira Cloud Forest may thus be due in part to competitive exclusion of later arrivals, regardless of the ecological amplitude and competitive ability of the latter. It might also be expected that species with wide ecological tolerance would tend to exclude species with narrower niches (see, for example, Lack, 1976).

Random colonization, unspecialized pollination systems, high seed-set, and competition for regeneration niches may thus be considered as possible determinants of the unique species assemblage and low species number in the Macuira Cloud Forest. There are other factors that should be entertained as well. First, the generations of the present Cloud Forest species may have undergone selection subsequent to their initial colonization; they may have lost some of their pioneering qualities and gained some attributes that are better suited to the Cloud Forest habitat. Second, the uniqueness of the assemblages of species in the Macuira, Santa Ana, and San Juan summit forests may be due in part to variation in the communities of herbivores and seed predators. Finally, the habitat itself may have characteristics, such as nutrient stress, that tend to cause impoverishment, as in the montane rain forests of Jamaica (Tanner, 1977, 1980).

Each of the possibilities considered above, except that of inherent impoverishment due to the combination of edaphic and climatic factors, is a function of isolation. This leads to the question of what is the most useful approach to the study of insular floras, in particular those that—like the Serranía de Macuira—are probably of relatively recent origin. With the advent of the equilibrium theory of island biogeography (MacArthur & Wilson, 1967), students of insular biotas became broadly split into two camps, with zoologists (especially ornithologists) adhering to the new mathematical models (see Simberloff, 1974) and botanists following the more traditional evolutionary and taxonomic paths (the recent symposium volume, *Plants and Islands* (Bramwell, 1979), contained only three passing mentions of the equilibrium theory). The equilibrium theory has been criticized in a general way by Sauer (1969), and its applications have recently been brought seriously into question by Gilbert (1980); both considered that the theory failed to take into account the biological complexity of insular ecosystems. This failure, especially with respect to studies based largely on species lists, was also pointed out by Connor and Simberloff (1978), who showed that the best

single predictor of species number was the number of collecting trips made to any particular island (in the Galapagos archipelago). Nevertheless, the more traditional botanical approach can also be faulted for its tendency to rely heavily on species lists and point samples made on single expeditions. The logical consequence of these criticisms is that more emphasis should be placed on longer-term studies of the ecology of island communities, alongside the continuing effort to improve taxonomic and distributional data concerning island species.

The approach of the present study has been biological, and the results, although largely derived from a species list, have provided some clues to the kinds of characteristics that might be expected of species constituting a flora of relatively recent origin. The insignificant level of endemism in the Macuira Cloud Forest flora has led to an appreciation of the importance of widespread variable species in insular situations—species that often receive inadequate attention in studies of insular floras with higher proportions of endemic species. These characteristics could not have been predicted by the equilibrium theory. I have not discussed whether the flora is at equilibrium, in the sense of MacArthur and Wilson (1967); given the nature of the sample and the impossibility of determining rates of colonization and local extinction, this would be a meaningless exercise. For the same reasons, and also because of the paucity of comparative data, the possible effects of area and distance from sources of propagules have not been considered; in any case, this would obscure some of the more important biological issues (see Gilbert, 1980).

Future work should be directed toward a greater understanding of these isolated summit forest communities on the Caribbean coasts of Colombia and Venezuela. The next step would be to investigate the possible determinants, outlined above, of the unique species assemblages and low species number in these forests. With the exception of random colonization, which is almost impossible to test empirically, the contribution of each factor (for example, pollination mechanisms, seed production, and availability of regeneration niches) could be assessed by observation and experiment in the field. Lastly, it should be emphasized that any such studies are enhanced by a firm taxonomic and chorological basis; the present study, which in a sense is a test of the adequacy of the taxonomic and distributional data concerning a small, random set of neotropical species, demonstrates the urgent need for further collections (accompanied by better notes) and improved taxonomic knowledge of the neotropical flora.

ACKNOWLEDGMENTS

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APPENDIX. **Notes on the taxonomy of Macuira Cloud Forest species.**

The following notes are brief summaries of the information that is available concerning the taxonomy of the species in the Macuira Cloud Forest flora that show

infraspecific variation, belong to a complex of two or more closely related species, or have dubious status as distinct species. Although the species are listed below under these three separate headings for convenience, it should be noted that some of them fit more than one of the categories. Fifty-nine of the 126 species in the flora are listed. Those not listed include species that show little or no infraspecific variation and have no close relationships (listed on p. 42), species that are distributed outside the neotropics (geographic element I), and species for which no information was found.

1. Variable species

Acalypha diversifolia Jacq. Pl. Rar. Horti Schoenbr. **2**: 63. *t. 244*. 1779. Variable in leaf size, shape, and pubescence. Three varieties distinguished (Pax & Hoffman, in Engler, Pflanzenr. IV. **147**(16): 107. 1924), according to amount and type of pubescence on leaves, petioles, and shoots.

Actinostemon concolor Mueller-Arg. in DC. Prodr. **15**(2): 1102. 1866. Seventeen varieties recognized (Mueller-Arg., *op. cit.*), differing in leaf shape. Sixteen varieties confined to southeastern Brazil, and one (var. *caribaeus*) to Lesser Antilles and Venezuela.

Anthurium scandens (Aublet) Engler in Martius, Fl. Brasil. **3**(2): 78. 1878. Variable species with one close relative (*A. trinerve* Miq.), together forming distinct group with overlapping distributions. Variation in *A. scandens* continuous; species best regarded as having no subdivisions (S. Mayo, pers. comm.).

Baccharis trinervis Pers. Synopsis Pl. **2**: 423. 1807. Great variation in leaf size and texture, and degree of pubescence on leaves and stems. Extremes of variation assigned to two varieties (Baker in Martius, Fl. Brasil. **6**: 73. 1844), var. *rhezoides* having smaller, densely pubescent leaves. Ranges of varieties overlap completely (Cuatrecasas, Revista Acad. Colomb. **13**: 49–55. 1967).

Campylocentrum micranthum (Lindley) Rolfe, Orchid Rev. **11**: 245. 1903. Variable in leaf size.

Cestrum alternifolium (Jacq.) O. E. Schulz in Urban, Symb. Antill. **6**: 270. 1910. Easily confused with *C. latifolium* Lam., which has more conical than cylindrical corolla and occurs in West Indies and tropical South America (Francey, Candollea **6**: 211. 1934). Closely related to *C. bogotense* Willd., of southern Andes of Colombia. Schulz described two varieties, differing slightly in floral dimensions: var. *pendulinum* (from Colombia eastward) and var. *mitanthum* (from Venezuela and Isla Margarita westward). Range of typical variety not stated.

Chiococca alba (L.) Hitchc. Ann. Rep. Missouri Bot. Garden **4**: 94. 1893. Variable in leaf size, inflorescence size, and habit. Varieties and subspecies distinguished (Steyermark, Mem. New York Bot. Garden **23**: 380. 1971) in terms of gradation from elongated, many-flowered inflorescences with well-developed peduncles through reduction series to few-flowered inflorescences, shorter peduncles, and smaller leaves. Typical subspecies represents many-flowered extreme and occurs throughout range of species.

Clidemia hirta (L.) D. Don, Mem. Wernerian Soc. **4**: 309. 1823. Variable in pubescence and in pattern of leaf margins. Macuira material resembles var. *elegans* (Aublet) Griseb., which has more crenulate margins and longer pubescence than typical variety.

Conostegia icosandra (Sw.) Urban, Repert. Sp. Nov. **17**: 404. 1921. Variable in pubescence. Northern Venezuelan (and Macuiran) specimens more glabrous than material from other regions (Wurdack in Lasser, Fl. Venezuela **8**: 523. 1973).

Costus guanaiensis Rusby, Bull. Torrey Bot. Club **29**: 694. 1902. Variable in form of pubescence on leaves and sheaths. Four varieties recognized (Maas, Fl. Neotrop. **8**: 51, 1972), of which three, including typical variety, have wide, overlapping distributions.

Dendropanax arboreus (L.) Decne. & Planchon, Revue Hort. IV. **3**: 107. 1854. Considerable plasticity of form, especially leaf shape and stature of mature individuals, according to habitat.

Desmodium axillare (Sw.) DC. Prodr. **2**: 333. 1825. Three intergrading varieties recognized (Schubert, Jour. Arnold Arb. **44**: 287. 1963), differing in leaf size and corolla color, with distributions overlapping in Antilles.

Encyclia fragrans (Sw.) Lemée, Fl. Guyane Fr. **1**: 148. 1855. Divided into two geographically replacing subspecies (Dressler, Phytologia **21**: 440. 1971): typical subspecies in Greater Antilles, southeastern Central America, and western Panama; subsp. *aemula* (Lindley) Dressler in Lesser Antilles, tropical South America, and eastern Panama. Also member of complex of 16 species, most with restricted or disjunct distributions within range of *E. fragrans* (Dressler, *op. cit.*).

Euphorbia cotinifolia L. Sp. Pl. **1**: 453. 1753. Variable in leaf shape, size, and color. Closely related to *E. caracasana,* which occurs throughout northern Andes and is considered (Webster & Burch, Ann. Missouri Bot. Garden **54**: 333. 1967) possible infraspecific form of *E. cotinifolia.* Leaves of Macuira material similar to those of specimens from Santa Marta, Colombia.

Ficus perforata L. Pl. Surinam. 17. 1775. Exceedingly variable species (de Wolf, Ann. Missouri Bot. Garden **47**: 154. 1960). Very similar to Antillean species *F. jacquiniifolia* A. Rich., *F. sintenisii* Warb., and *F. perforata* L.

Guapira fragrans (Dum.-Cours.) Little, Phytologia **17**: 368. 1968. Variable in leaf shape and size; variation shows no geographic pattern, and entire range of leaf size and shape sometimes seen on one individual.

Guzmania lingulata (L.) Mez in DC. Monogr. Phanerog. **9**: 899. 1896. Five varieties maintained (L. B. Smith, Fl. Neotrop. **14**: 1349. 1977), differing in plant size, flower number per inflorescence, and involucral bract orientation and color. Typical variety, which Macuira material resembles, occurs throughout range of species; other varieties have narrower distributions.

Guzmania sanguinea (André) André ex Mez in DC. Monogr. Phanerog. **9**: 901. 1896. Exhibits varietal differences in shape of floral bracts (L. B. Smith, Fl. Neotrop. **14**: 1334. 1977).

Heliconia bihai L. Mant. Pl. **2**: 211. 1771. Variable, polymorphic species (L. Andersson, pers. comm.).

Malvaviscus arboreus Cav. Monad. Cl. Diss. **3**: *t. 48.* 1787. Variable in overall size (treelet 2–10 m tall), petal shape.

Miconia acinodendron (L.) Sweet, Hortus Brit. **1**: 159. 1826. Variable in leaf pubescence. Plants from cloud forest in Yaracuy, Venezuela (Wurdack in Lasser, Fl. Venezuela **8**: 429. 1973) and Serranía de Macuira have near-glabrous leaves and may differ infraspecifically from material from other regions (Wurdack, *loc. cit.*).

Miconia laevigata (L.) DC. Prodr. **3**: 188. 1828. Varies infraspecifically in many characters; subspecific evaluation may be required (Wurdack in Lasser, Fl. Venezuela **8**: 382. 1973).

Myrcia fallax (Rich.) DC. Prodr. **3**: 244. 1828. Highly variable in many characters.

Myrcianthes fragrans (Sw.) McVaugh, Fieldiana Bot. **29**: 486.⁷1963. Very variable in petiole characters, leaf blade width, and flower number per dichasium (McVaugh, *loc. cit.*).

Pilea microphylla (L.) Liebm. Danske Vidensk. Selsk. Skrifter **5**(2): 296. 1851. Variable in size, habit, and leaf size; closely allied to three other species with more restricted range (Killip, Contr. U. S. Natl. Herb. **26**: 477. 1939).

Pleurothallis ruscifolia R. Br. in Aiton, Hortus Kew. ed. 2. **5**: 211. 1813. Floral segments continuously variable (Foldats in Lasser, Fl. Venezuela **15**(2): 392. 1970).

Polystachya foliosa (Lindley) Reichenb. f. in Walp. Ann. Bot. Syst. **6**: 640. 1864. Variable in size, and closely related to *P. flavescens* J. J. Sm. (widespread tropical species).

Psychotria alba Ruiz & Pavon, Fl. Peruv. **2:** 58. 1799. Generally confused and mis-
identified in herbaria (Steyermark, Mem. New York Bot. Garden **23:** 228. 1972)
due to close resemblance to *P. horizontalis* Sw. (variable species widespread in
neotropics) and to *P. carthaginensis* Jacq. (also widespread but absent from West
Indies). Inclusion of *P. alba* with *P. carthaginensis* recommended by Smith and
Downs (Jour. Washington Acad. **48:** 284. 1958).

Psychotria barbiflora A. DC. Prodr. **4:** 509. 1830. Variable in length and shape of
bracts, and closely related to *P. hoffmanseggiana* (Steyermark, Mem. New York
Bot. Garden **23:** 602. 1972).

Psychotria nervosa Sw. Prodr. 43. 1788. Very variable in leaf and corolla pubes-
cence. Two subspecies maintained (Steyermark, Mem. New York Bot. Garden **23:**
479. 1972), with almost completely overlapping distributions. Typical subspecies
represents glabrous extreme; subsp. *rufescens*, which Macuira material resembles,
has densely pilose or villosulous corolla and is commoner subspecies in Colombia
and Venezuela.

Randia formosa (Jacq.) Schum. in Martius, Fl. Brasil. **6:** 342. 1889. Variable, es-
pecially in length of corolla and calyx tubes. Three varieties maintained (Steyer-
mark, Mem. New York Bot. Garden **23:** 327. 1972) with fairly distinct distribu-
tions.

Renealmia occidentalis (Sw.) Sweet, Hortus Brit. **2:** 493. 1830. Two varieties rec-
ognized (Maas, Fl. Neotrop. **18:** 103. 1977), differing in peduncle length, fruit
size, and flower number per inflorescence. Closely related to *R. floribunda* K.
Schum., which occurs in humid parts of Amazon basin, Guianas, and Trinidad.

Vriesea splendens (Brongn.) Lem. Fl. Serres **6:** 162. 1851. Four varieties maintained
(L. B. Smith, Fl. Neotrop. **14:** 1217. 1977) according to leaf variegation. Macuira
material resembles var. *formosa*, which occurs throughout range of species.

Xiphidium caeruleum Aublet, Pl. Guian. **1:** 33. 1775. Variable in many characters.

2. SPECIES OF DUBIOUS TAXONOMIC STATUS

Cordia macuirensis Dugand & I. M. Johnston, Caldasia **7:** 107. 1955. Endemic to
Serranía de Macuira, but very closely related to *C. curassavica* (Jacq.) Roemer
& Schultes, which is widespread in neotropical dry lowlands and common on sandy
slopes on northwestern sides of Serranía de Macuira. Differs from *C. curassavica*
in its smaller, glabrous leaves, pulverulent to glabrous calyx, and higher ratio of
corolla length to calyx length. *Cordia curassavica*, however, shows phenotypic
variation, with small-leaved xerophytic form and large-leaved mesophytic form;
C. macuirensis may be incipient species. In Serranía de Macuira, maintenance of
reproductive isolation between these two species must depend on constancy of hab-
itat preferences of insect pollinators, since flowering periods overlap and *C. cur-
assavica* is self incompatible (Opler, Baker, & Frankie, 1975).

Croton margaritensis J. R. Johnston, Proc. Am. Acad. **40:** 690. 1905. Very closely
related to *C. populifolius* P. Miller (Johnston, *loc. cit.*), which is common in north-
ern lowland Venezuela and Colombia; differs from latter in having shorter bracts
and stipules and more lanceolate leaves, and in lacking petals in pistillate flowers.
More critical analysis of these species required, in view of apparent disjunct dis-
tribution of *C. margaritensis* (in Serranía de Macuira and Isla Margarita) and its
close relationships with more widely distributed *C. populifolius*.

Elleanthus arpophyllostachys Reichenb. f. in Walp. Ann. Bot. Syst. **6:** 479. 1862.
Closely related to *E. columnaris* (Lindley) Reichenb. f., which is slightly more
robust and occurs in Colombia and Venezuela, 2000–2800 m (Foldats in Lasser,
Fl. Venezuela **15**(1): 209. 1969). May be varieties of same species (Foldats, *op.
cit.*), varying phenotypically according to altitude.

Epidendrum agathosmicum Reichenb. f. Linnaea **22:** 841. 1849. Identification of
Macuira material tentative due to paucity of flowering material. Similar and closely

related to *E. polyanthum* Lindley, which occurs in Mexico, Central America, Venezuela, and Brazil (Foldats in Lasser, Fl. Venezuela **15**(3): 169. 1970).

Genipa spruceana Steyerm. Mem. New York Bot. Garden **23**: 353. 1972. Separated from *G. americana* L. (widespread neotropical species) on basis of calyx tube with mainly glabrous interior and thin, noncallose margin, degree of pubescence on inner surface of corolla, and thinner, glabrous, lustrous leaves (Steyermark, *loc. cit.*). Serranía de Macuira well outside northern Amazonian range of *G. spruceana*, but within range of *G. americana*. Characters distinguishing species minor; *G. spruceana* and *G. americana* might be better considered as single variable species.

Guettarda divaricata (Humb. & Bonpl.) Standley, Publ. Field Mus. Bot. **7**: 403. 1931. Closely related to (possibly not distinct from) *G. parviflora* Vahl, which occurs in West Indies, Guianas, and Venezuela (Standley, *op. cit.*). Also closely related to *G. odorata* (Jacq.) Lam. of West Indies, *G. elliptica* Sw. of Greater Antilles, Florida, and Mexico, and *G. rusbyi* Standley of Colombia (Steyermark, Mem. New York Bot. Garden **23**: 361. 1972).

Maranta divaricata Roscoe, Monandr. Pl. *t.* 27. 1828. Variable in leaf color (Schumann in Engler, Pflanzenr. IV. **48**: 126. 1902) and closely related to widespread neotropical *M. arundinacea*. Doubtful whether former is more than poor variety of latter (Standley & Steyermark, Fieldiana Bot. **24**: 218. 1952).

Philodendron erubescens C. Koch & Augustin, Index Sem. Hort. Bot. Reg. Berol. Collect. App. 6. 1854. Described from cultivar; field collections so scarce that natural distribution unclear. Appears closely related to *P. krugii* Engler, which occurs in Trinidad. Macuira material sterile.

Polypodium maritimum Hieron. Bot. Jahrb. **34**: 527. 1904. Very similar to *P. loriceum* L. (widespread, variable species).

Schlegelia fuscata A. Gentry, Ann. Missouri Bot. Garden **60**: 925. 1973. Possibly local form of *S. parviflora* (Oersted) Monachino, which occurs in moist lowlands of Central and South America (Gentry, *loc. cit.*) and is very variable in several characters. Former differs most conspicuously from latter in having more or less racemose inflorescence and extremely coriaceous leaves.

Solanum dulcameroides Dunal in Poiret, Encycl. Suppl. **3**: 751. 1813. Closely allied to *S. seaforthianum* André (pan-Caribbean species) (W. G. D'Arcy, pers. comm.); relationships between these species and their allies poorly understood.

Zamia muricata Willd. Sp. Pl. **4**: 847. 1805. Macuira material tentatively identified, in absence of good collections and adequate monographic treatment of *Zamia* in tropical America.

3. SPECIES BELONGING TO GROUPS OR COMPLEXES OF TWO OR MORE CLOSELY RELATED SPECIES

Anthurium crassinervium (Jacq.) Schott, Wiener Zeitschr. Kunst Lit. Theater Mode **1829**: 828. 1829. Member of complex of ca. 15 species that as group have pan-Caribbean distribution (S. Mayo, pers. comm.). Differences between them slight, perhaps suggesting recent and continuing divergence due to geographic isolation. Habitat-related diversity of form is common in complex.

Blechnum arborescens (Klotzsch & Karsten) Hieron. Hedwigia **47**: 239. 1908. Related to *B. schiedianum* (Presl) Hieron., which occurs in Andes of Ecuador and southern Colombia. Differs mainly in degree of purplish coloring of rachis and leathery pinnae. Also similar to *B. lineatum* (Sw.) (montane Antillean species).

Chamissoa altissima H.B.K. Nova Gen. Sp. Pl. **2**: 197. 1817. Closely related to *C. macrocarpa* H.B.K., which is restricted to Amazon basin (J. A. Duke, Ann. Missouri Bot. Garden **48**: 21. 1961).

Cynanchum atrovirens (Rusby) Sugden. Closely related to *C. parviflorum* (R. Br.) Alain, which occurs in Lesser Antilles, Venezuela, and Colombia. Most distinctive

feature separating these species is abundance of short (0.5 mm) hairs covering entire interior corolla of *C. atrovirens* (Dugand, Caldasia **9**: 444. 1966).

Grammitis blepharolepis (C. Chr.) Morton, Contr. U. S. Natl. Herb. **38**: 98. 1967. Closely related to *G. daguensis* (Hieron.) Morton (lowland Cauca and Valle, Colombia) and *G. trichomanoides* (Sw.) Ching (West Indies) (Morton, *op. cit.*).

Guzmania cylindrica L. B. Sm. Phytologia **5**: 282. 1955. First described from specimen from Serranía de Macuira. Closely related to *G. mucronata* Mez, which is restricted to low-altitude cloud forest in northern Venezuela (L. B. Smith, *op. cit.*).

Jacquiniella globosa (Jacq.) Schlechter, Repert. Sp. Nov. **7**: 124. 1920. Closely allied to *J. colombiana* Schlechter, from Cauca, Colombia, but differing in labellum shape.

Machaerium humboldtianum Vogel, Linnaea **11**: 194. 1837. Member of complex of at least six species with various neotropical distributions (V. E. Rudd, pers. comm.).

Persea caerulea (Ruiz & Pavon) Mez, Jahrb. Bot. Gart. Berlin **5**: 171. 1889. One of seven closely related species. *Persea caerulea* shows clinal variation in leaf shape (Kopp, Mem. New York Bot. Garden **14**: 34. 1966).

Scutellaria verecunda Epl. Feddes Repert. **85**: 173. 1936. One of group of five closely allied species, all except *S. verecunda* having wide overlapping distributions. Possible that these species are varieties or subspecies of single variable species (Epling, Univ. Calif. Publ. Bot. **20**: 1–146. 1942).

Stemmadenia minima A. Gentry, Ann. Missouri Bot. Garden **64**: 322. 1977. Closely related to *S. allenii* Woodson, which occurs west of Panama Canal Zone and Costa Rica, and to *S. lagunae* Woodson, known only from Bocas del Toro, Panama.

Utricularia alpina Jacq. Enum. Pl. Carib. 11. 1760. One of five closely allied tropical American species (Taylor, Ann. Missouri Bot. Garden **63**: 569. 1976).

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